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LIMITING FACTORS IN RELATION TO SPECIFIC
RANGES OF TOLERANCE OF FOREST
TREES

A. H. HUTCHINSON

(WITH SEVEN FIGURES)

The conclusions recorded in this paper are drawn from a study of the forests throughout the Province of Ontario, particularly along the shores of Lake Ontario, Lake Simcoe, the Kawartha Lakes, and Rideau Lakes; in Algonquin Park and in Mattagami and Timagami Forest Reserves. Observations, with notes, have been made during more than 6000 miles of travel by canoe and overland through the forest country of northern Ontario, especially along the streams and lakes forming the headwaters of the Muskoka, Maganatawan, Petewawa, and Madawaska rivers; also of the Montreal, Sturgeon, Wanapitei, Vermilion, Mattagami, and Abitibi rivers. While the greater part of the discussion has particular reference to Ontario, the conclusions are made in the light of some personal knowledge of the forests southward to the Gulf of Mexico and westward to the Pacific.

The data regarding the limits of forest trees recorded in the accompanying maps have been obtained principally from accounts of the explorations of BELL (2), MACOUN (19, 20), and LOW (18). The records of isotherms and precipitation areas have been copied from the Geological Atlas of Canada, 1915. So far as the writer

has been able to observe, the records of the explorers mentioned have been even more accurate than has generally been conceded. Although the specific limits of forest species have been rather definitely outlined, there seems to be no agreement regarding the part played in determining these limits by the various factors affecting forest growth. In this paper an attempt has been made to relate the limiting factors to the specific range of tolerance of forest trees, and in this way to account for the respective distributions of some of the species dominating the forests of Ontario.

SCHIMPER (21), as a result of his extensive studies in plant geography, concludes that "the differentiation of the earth's vegetation is thus controlled by 3 factors: heat, atmospheric precipitation (including winds), soil. Heat determines the flora, climatic humidity the vegetation; the soil as a rule merely picks out and blends the materials supplied by these two climatic factors, and on its own account adds a few details."

Investigators have mentioned many factors which affect the composition of forests. Drawing his conclusions from the exploration of Labrador, Low (18) says "the distribution of forest areas and the range of the various trees depend upon several factors, among which may be mentioned position as regards latitude, height above the sea coast, and the character of the soil." BOWMAN (3) in the light of his physiographic studies says as follows:

The distribution of forests is controlled largely by rainfall, although the distribution of species within each region is also controlled by insolation, temperature, wind velocity, water supply, and geographic relation to post-glacial centers of distribution. When more detailed statements are attempted many difficulties are encountered in the form of apparent inconsistencies. Some species appear to find their appropriate conditions in different latitudes by a change in their habitat; for example, the larch, balsam fir, and white birch which in the north grow freely on dry or hilly ground, toward the southern limits seek the cold ground in swamps. The white cedar and white pine in some places manifest the same tendency.

FROTHINGHAM (12) in his report on hardwood forests sums up the situation as follows: "How moisture and temperature affect the different species in the complexity of forest environment is still so little known that no positive information can be given."

Temperature factor

The northern limits of many tree species are undoubtedly the result of low temperatures. WARMING (24) states, "It is clear that conditions as regards heat determine the boundaries of the distribution of species on the earth." The effect of temperature is emphasized by the fact that "the appropriate temperature for the growth of a number of species, such as *Picea* and *Abies*, is carried far to the south of their normal latitudes along the elevated parts of the continent, especially the Alleghanies and Rocky Mountains" (BELL 2). In such regions the tree species are in most cases identical with those found farther north. However, it is more difficult to account for the southern limits of trees on a basis of minimum temperature. BRAY (5) finds difficulty in explaining the occurrence of boreal (*Picea*, *Abies*) associations in the bogs of regions dominantly austral. "The question arises as to whether the factor of temperature plays a rôle in the occurrence of these bogs," and again, "the extremely irregular boundary between the boreal conifer forests and the temperate hardwood forests of New England, for example, can hardly be explained by temperature alone" (HARPER 14).

The lines representing the limits of *Picea nigra*, *Larix americana*, and *Betula papyrifera* follow yearly isotherms very closely from the mouth of the Mackenzie River across the continent until they reach the coast of Labrador, where they swing southward, here following a course almost parallel with the coast line. There is reason to believe that temperature is the limiting factor throughout a great area, while a second factor is active along the Labrador coast. From the fact that the same order in the limitation of these species is retained, even in the Labrador region, it would seem that the limiting factors are similar throughout. Excessive loss of heat energy due to the air currents so prevalent in this region has the same effect as the loss of heat energy due to excessively low temperatures. Similarly in southern Ontario, where latitude and lake influence together result in a region of a relatively high yearly temperature average, the limits of trees such as *Juglans nigra* and *Castanea dentata* are parallel with isotherms. Here also the evidence would indicate that temperature is the limiting factor with

respect to such species. The general conclusion that temperature is usually, if not universally, the determinant of northern limits has resulted from making general statements based upon selected and favorable instances which are specific rather than general.

There is abundant evidence that while temperature acts as a limiting factor in many instances, it is by no means the only factor controlling even the northern limits of tree species. This is amply demonstrated by the data recorded on the accompanying map (fig. 1). Many of the lines indicating the northern limits of tree species intersect; this cannot be accounted for on a temperature basis. Isotherms do not intersect nor do lines indicating the length of the growing season. The northern limit of *Pinus Banksiana* at 100° W. long. traverses a region the yearly isotherm of which is 25° F.; at 80° W. long. the isotherm which the northern limit traverses is 32.5° F.; at 75° W. long. it is 20° F.; and at 70° W. long. it reaches the 32.5° F. isotherm. The isotherms corresponding to the northern limits of *Ulmus americana* at various regions are at 100° W. long. 27.5° F.; at 95° W. long. 32.5° F.; at 80° W. long. 30° F.; at 75° W. long. 40° F.; and at 70° W. long. 32.5° F., a remarkable range of variation. The looping of the lines representing the limits of such species as *Picea canadensis*, *Populus balsamifera*, and *Populus tremuloides*, as shown in the Labrador region (northern Quebec), is significant, particularly in the case of *Picea canadensis*, in contrast with the closely related *Picea mariana*. The northward deviation of the limits for *Betula lutea*, *Acer saccharum*, *Tsuga canadensis*, and *Quercus rubra* at 80° W. long., a point where the isotherm swings southward, cannot be explained on a temperature basis. The anomalous tree distribution in the Saugenay region is another case in point. Any idea of the possibility of explaining the western limits on a temperature basis has long been discarded. It is evident that in the instances mentioned something other than temperature must be the limiting factor.

Water factor

Water as a factor in the determination of tree distribution has received considerable recognition. COWLES (8) says, "On the whole there has been a general tendency to overestimate the influence of

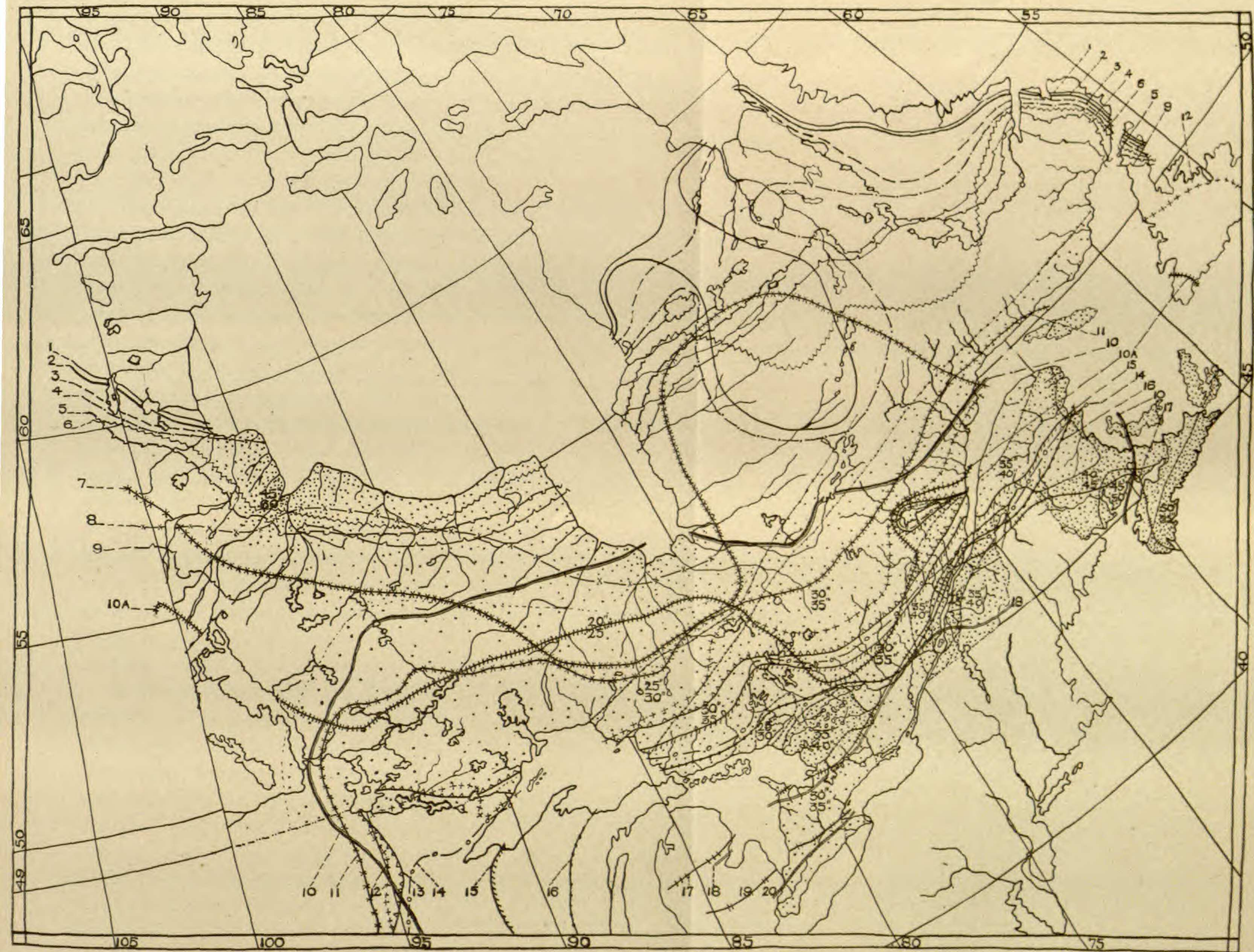


FIG. 1.—Northern limits of tree species represented by lines having identification numbers and marks: *o*, original; *r*, revised; isobars outlined by connected dots and average yearly temperature indicated in degrees; 1, *Picea mariana*; 2, *P. canadensis*; 3, *Larix americana*; 4, *Populus balsamifera*; 5, *Betula papyrifera*; 6, *Populus tremuloides*; 7, *Pinus Banksiana*; 8, *P. Banksiana* (other data and outliers); 9, *Abies canadensis*; 10, *Thuja occidentalis*; 10A, *Ulmus americana*; 11, *Pinus Strobus*; 12, *Betula lutea*; 13, *Acer saccharum*; 14, *Quercus rubra*; 15, *Tsuga canadensis*; 16, *Fagus americana*; 17, *Juglans cinerea*; 18, *Carya amara*; 19, *Juglans nigra*; 20, *Castanea dentata*.

temperature as an ecological factor. The trend of nearly all experiment has been to show that water is of vastly greater importance." BELL (2) states, "A great difference in the moisture of the air of two regions otherwise resembling each other in climatic conditions has also a powerful effect upon the growth of forests; and the dryness of the air in the western prairie and arid regions is, no doubt, the chief cause of the absence of timber."

There has been much recent research concerned with the water relation of plants (9). The greater number of investigators have selected the region of the great plains, a region where water is dominantly the limiting factor, as their field of investigation. TRANSEAU (22, 23), LIVINGSTON (16, 17), and FULLER (13) have shown that the water factor may be regarded as a complex depending primarily upon the amount of soil water available for the plant and the rate of evaporation. The amount of available soil water is dependent upon precipitation during the growing season and the physical properties of the soil, while evaporation depends chiefly upon the humidity, air currents, and temperature of the atmosphere. BRIGGS and SHANTZ (4) in their work on the wilting coefficient have emphasized the specificity of tolerance in plants with respect to minimum soil water. The valuable experimental data recorded in these papers demonstrate that water frequently acts as a limiting factor; the converse, that there is a considerable range for any given species wherein water does not factor in a limiting capacity, is less frequently emphasized.

It is significant that the limits of tree species such as *Picea mariana*, *P. canadensis*, *Larix americana*, *Populus balsamifera*, *Abies canadensis*, and *Betula papyrifera*, which extend north of the arid plains, are not deflected southward in the Manitoba-Minnesota region, while almost invariably the more southern species are deflected when they come in contact with the region of diminished precipitation. The evidence would indicate that the water factor limits the westward extension of such species as *Acer saccharum*, *Tsuga canadensis*, *Fagus americana*, *Thuja occidentalis*, and *Ulmus americana*.

It may be noted, also, that when this deflection takes place the order in which the tree limits occur is changed in many instances.

Thuja occidentalis, which extends northward far beyond *Acer saccharum*, does not reach the western limits of the latter, while *Quercus rubra* extends westward beyond the limits of many species which are to be found beyond its northern limit. Such phenomena doubtless are the result of the fact that different limiting factors dominate the several regions forming the boundaries of distribution.

In southeastern Canada it is difficult to find any parallelism between the limits of tree species and the boundaries of precipitation areas. For instance, *Juglans cinerea* extends throughout areas whose respective yearly precipitations are 30-35 in., 35-40 in., 30-35 in., 40-45 in., and 45-50 in., with no apparent deflection of the lines bounding its growth area. The limits of *Fagus americana* pass through similar areas, with the addition of an area where the minimum yearly precipitation is 25 in. This range is of particular significance in consideration of the fact that *Fagus* is generally regarded as mesophytic. The absence of a parallelism between precipitation and forest limits in the Ontario section is so obvious from a consideration of the accompanying map (fig. 2) that further emphasis would be superfluous. Other conditions being favorable, there is sufficient rainfall for forest growth; or, in other words, precipitation does not enter here as a limiting factor.

WARMING (24) has based his ecological classification of plants upon the premise that "the most potent and decisive factor is the amount of water in the soil." "The soil upon which the coniferous forest occurs varies widely, yet so far as reliable information is available it is always physically or physiologically dry." "The cold winter is a physiologically dry season against which trees can protect themselves by defoliation or by xerophytic structure." This may account for the xerophytic structure of the coniferous leaf; it is difficult to understand what bearing it has in connection with the contention that conifers as a class grow in dry soil conditions, the winter, even for conifers, being a period of comparative dormancy. Deciduous trees are protected against the "physiological dryness" of winter by leaf fall; conifers by having leaves of xerophytic structure. Some deciduous trees, for example *Quercus*, are comparatively xerophytic, while others are decidedly meso-

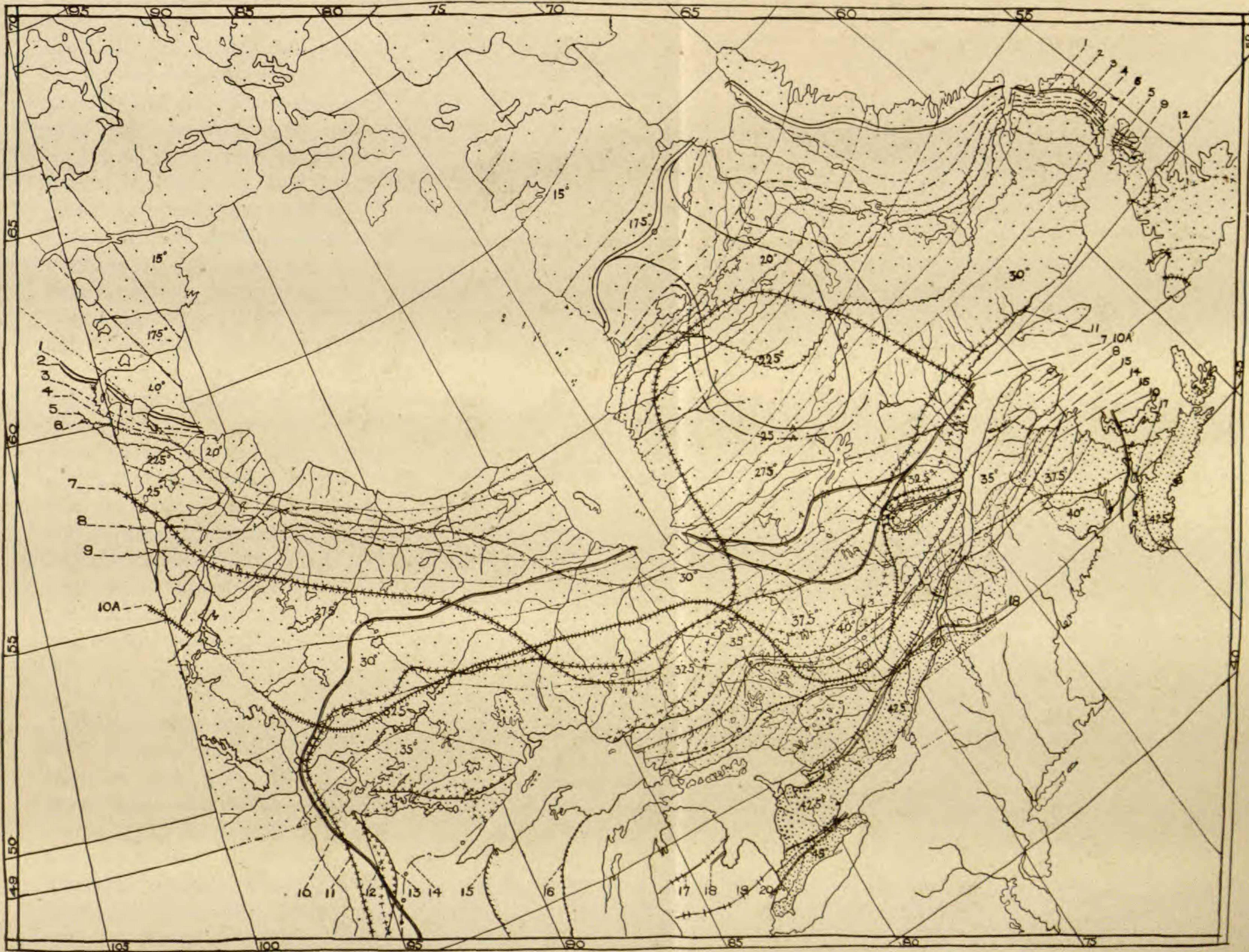


FIG. 2.—Similar to fig. 1 except that a precipitation rather than a temperature map is superimposed upon the chart of tree limits; numbers indicate precipitation in inches.

phytic, as *Fagus* and *Acer*. It seems possible that there might be a similar range amongst conifers. ZON (27) states, "Balsam fir attains its best growth and largest size on flats the soil of which is usually a moist, deep sand-loam." An abundance of available soil water is not the factor which so often excludes *Abies balsamea* from such soils, particularly in the more temperate regions.

During the summer of 1914 a series of experiments were conducted in Algonquin Park to discover the relation of seedling growth to atmospheric humidity. Atmometers of the LIVINGSTON design were set up at a number of stations, including those where seedlings of *Acer saccharum*, *Abies balsamea*, and *Picea mariana* were abundant. The readings for the months of July, August, and part of September proved that in this region there is no appreciable difference in the rates of evaporation at the stations mentioned, and that in each case the humidity was in excess of that which FULLER (13) regards as characteristic of a mesophytic forest. Moreover, *Acer* grows on the more exposed ridges; *Abies* and *Picea* on the less exposed lowlands or slopes. Experiment has shown that such conditions hold generally for the "lake country," where in many cases one-tenth of the total area is covered by water, and the greatest distance of any point from bodies of water seldom exceeds 2 miles. Three of the limiting factors most frequently emphasized, temperature, atmospheric humidity, and precipitation, are eliminated, as such, under conditions prevailing, and still there is a marked segregation of forest associations.

Soil factor

The problem regarding the extent to which soil composition may act as a limiting factor in the determination of forest distribution has been variously answered. FROTHINGHAM (12) states "The soils of the northern hardwood forest are as a rule loamy sands, the results of the decay of granite, quartzites, and siliceous gneisses, also the water assorted loams and clays or the unassorted morainal tills, rich in clay; but they also thrive on light sandy soil in localities subject to moist winds." In connection with the forests of Michigan, BEAL and WHEELER (1) state that "The best wheat lands are usually found on uplands near

streams, where the oak timber gradually shades into beech and maples." On the other hand, "evergreen trees, whether coniferous or broad-leaved, seem to be just as characteristic of poor soil as of any particular kind of climate" (14). BOWMAN (3) draws attention to the limitations of soil composition as a determining factor. COWLES has shown that the composition of the rock from which any soil may be derived seldom acts in a limiting capacity with respect to the species which that soil may support. It is only in exceptional cases that a soil, newly weathered, is deficient in the mineral constituents necessary for plant growth. This generalization is particularly applicable in Ontario, where the soil, whether it be glacial drift toward the south, or the weathered deposits and exposed rocks farther north, is derived from the dominantly granitic rock of the Laurentian Plateau. The original composition of the soil is seldom a limiting factor, at least in so far as the forests of Ontario are concerned.

Humus factor

It is scarcely necessary to emphasize the importance of the humus content of the soil as an ecological factor; its significance as a limiting factor with respect to the forests of Ontario is our chief concern. In forest regions the humus content of the soil increases the water retaining capacity; increases the porosity, and hence the aeration of the soil. Mineral salts are retained by the adsorptive properties of humus, and incidentally, conditions are made more favorable for soil bacteria, which are essential for the growth of such species as *Fagus*. COWLES (8) states, "Although bare sand supports a xerophytic flora, the accumulation of a thin humus layer is sufficient for forest development, and the Michigan dunes show that the most mesophytic of our forests can grow on a sand dune if there is present a humus layer a few centimeters in thickness." In the Algonquin Park region to which reference has been made, the *Acer* or *Acer-Fagus* forest occupies the ridges, while the *Abies-Picea* forest occupies the lower slopes and lowlands. On the slopes where the exposure of the rocks, due to drainage of glacial lakes, has been comparatively recent, only a small amount of rock soil has accumulated; this is covered by a humus layer, but the two are not intimately intermingled by weathering processes. The

humus content of the soil proper is low. In the lowlands a similar condition maintains. This is especially applicable to the peat bog, where humus is most abundant. There has been no movement, however, of the particles of the contiguous strata of the rock soil and the overlying humus; they are distinct, hence the otherwise valuable humus is practically useless in so far as the improvement of soil properties is concerned. On the ridges which were exposed first by the subsidence of glacial ice and water there is much deeper soil, and the humus accumulated from antecedent vegetation has become intimately associated with the rock soil by weathering. The soil proper has a high humus content and is able to support such trees as *Acer* and *Fagus*. It will be remembered that the temperature, precipitation, humidity, and original soil composition may be regarded as constant; the varying factors are those associated with the accumulation of humus. The humus content of the soil is at least a local factor in the determination of tree distribution.

It has been maintained that differences in the composition of soil have only a local effect. It does not seem clear why a factor which is potent locally should not be potent throughout greater areas. The gradients of soil changes are usually greater when limited areas are considered; hence also those of the associated floral changes. The Laurentian Plateau is a great area dominated by the coniferous forest, while the contiguous region of glacial drift is dominated by the deciduous hardwood forest. The marked differences in forest species prevailing in the regions north and south of the Kawartha Lakes, respectively, is strikingly in accord with soil differences. Moreover, the line separating the dominantly coniferous region from the dominantly deciduous hardwood region does not follow any isotherm or the boundaries of any precipitation area, but rather the outlines of the Laurentian Plateau, roughly from the southeast part of Georgian Bay to Lake Simcoe along the Kawartha Lakes, southeastward to the Thousand Islands, northward to Ottawa, and again eastward along the northern limits of the Ottawa and St. Lawrence valleys. In the coniferous region there are oases of deciduous hardwoods of considerable area, such as that at Renfrew, or of limited area, such as the ridges already mentioned; in fact, wherever the soil is similar to that found in the

characteristically deciduous hardwood area. It is true that these broad outlines have been obscured in many places by large tracts being covered with pioneer forms, such as *Populus* and *Betula*, as a result of "burns" (10, 11, 15). These regional forest limitations cannot be explained except upon some basis of soil differences, such as have been described as determining the local limitations of the forest types of Algonquin Park. The evidence clearly indicates that the slowly weathering rock of the Laurentian Plateau has been a barrier against migration of the hardwood forest, which, however, has been able to establish outposts where favorable soil conditions have been found. In brief, the development of a soil, particularly with reference to its humus content, may act as a limiting factor regionally as well as locally.

Light factor

It is generally accepted that seedlings of some tree species grow only where there is abundance of light, while others grow best under shade conditions (26). FROTHINGHAM (12) has classified the trees of the northern hardwood forest upon the basis of light tolerance. The seedlings of pioneer species are necessarily light tolerant in contrast with those species forming the climax forest, which are shade tolerant; seedlings of *Pinus Banksiana* and *P. Strobus* thrive only in direct sunlight, which is also the case with seedlings of *Abies balsamea* and *Picea canadensis*, although to a less marked degree. On the other hand, the seedlings of *Acer* and *Fagus* grow best in the dense shade of mature trees; *Tsuga canadensis* is an example of a conifer which is similar in this respect. Because of the specificity of the range of tree species with respect to intensity of light, certain forms cannot be pioneers, while others are eliminated from forests which have been well established, except where destructive agencies such as cause windfalls and erosion are at work. To this extent the intensity of light may act as a limiting factor in tree distribution.

Time factor

The time factor deserves a most important place in any consideration of the distribution of forest trees, and it is of particular significance in connection with the forests of Ontario. Time as a

factor in limiting the distribution of forest species is an expression of the rate of change in ecological conditions and of the specific rates of migration of the various species. Ordinarily conditions change so slowly that migration keeps pace; when there are more rapid changes migration lags behind. The time factor, therefore, must be considered in relation to the rate of change of such conditions as temperature, water, soil, light intensity, and secondarily in relation to methods of distribution.

WARMING (24) states, "Changes in the physical relationship of the soil are everywhere and always taking place, and in close correlation with this plant communities also undergo modification, but it does not seem possible to use development as the fundamental basis of classification of plant societies." COWLES (7), while recognizing the same factors, attaches more importance to development of successional associations.

The forests of Ontario have been made possible only by the retreat of glacial ice and water and the establishment of conditions permitting the growth of trees. It is evident that modifications of temperature have been prerequisite for the northward migration of tree species; by many it is regarded as the only factor. ADAMS suggests that the northern migration following the retreating glacier would comprise 3 great waves of life: (1) a wave of glacial or arctic vegetation, of which there are remnants in New York and Mount Marcy and two or three other high peaks; (2) a wave comprising the northernmost species of trees, stunted willows, birches, alders, and the coniferous forest spruces, hemlock, and pines; (3) a wave embracing the temperate zone deciduous trees. HARSHBERGER records a similar conclusion: "Several great waves of plant migration may be recognized, namely, glacial vegetation, tundra coniferous forests, and a migration of the deciduous forest elements from the southeastern center." If forest migration has kept pace with temperature changes, it might be expected that the limits of forest species would conform in outline with respective isotherms. It has already been demonstrated that in many instances this is not the case. The conclusion that in many places the migration of such species as *Tsuga canadensis*, *Acer saccharum*, and *Fagus americana* has lagged behind temperature changes is

made necessary. To a greater or less extent this is true of all the species forming the forests of Ontario. Under existing temperatures any further migration is dependent upon changes in the conditions now acting as limiting factors, as water, soil, and light. The rate of migration, and hence the distribution of forest trees, is dependent, primarily, upon the rate of change in temperature; however, migration may be restricted by other factors.

There is reason to believe that the yearly precipitation has gradually decreased since the glacial epoch. The data regarding the exact extent of these changes are limited. There can be no doubt, however, that the westward migration made possible by temperature changes has been checked by the water factor; also the irregularity of the limits of *Pinus Banksiana* may be explained by the fact that although temperature conditions have so changed that this species has migrated to 56° N. lat. in the highlands of northern Quebec, it has been limited in its northward progress by the low lying lands south and westward from James Bay. The inconsistencies of data regarding the northward distribution of *Pinus Banksiana* are doubtless due to the presence of certain outliers which might be expected when available soil moisture and other soil conditions act as the limiting factor, but which would be most improbable were temperature the determining factor of distribution. In regions where water is a limiting factor the rate of migration is dependent upon the rate of change in water conditions, in other words, upon the time factor.

Time factor in relation to soil development

It has been demonstrated that soil development, particularly with reference to the humus content, is a potent factor in determining the boundaries separating the *Acer-Fagus* and the *Abies-Picea* forests of Ontario. Since the *Acer-Fagus* forest demands the most highly developed soil, we are forced to the conclusion that in a forest succession the deciduous hardwood forest is the climax type. Over a vast area this climax type of forest has been excluded by soil conditions rather than by temperature. Northward migration of the deciduous hardwood forest has been limited by the rate of soil changes rather than by the rate of temperature

changes; with respect to the latter migration has lagged behind. Upon such a basis the "anomalous" separation of the deciduous hardwood forest and the coniferous forest is readily explained. The granitic rock of the Laurentian Plateau has weathered slowly, humus has accumulated slowly; in brief, the soil has developed slowly, hence the migration of the climax forest has been checked. This principle applies regionally as well as locally. In the region of glacial moraines the deep soil has made possible a rapid accumulation of humus, as well as a thorough intermingling of rock soil and humus. There has been a rapid development of the soil, consequently the *Acer-Fagus* forest has been permitted to invade such regions. The time factor as an expression of the rate of soil development has limited the rate of migration and hence forest distribution also.

The time factor in relation to soil development explains both the numerous northerly outliers of *Acer* associations and also the outliers of the *Picea-Abies* forest. The northward deviation of the limits of such species as *Acer saccharum*, *Fagus americana*, and *Tsuga canadensis* has been noted. It is significant that this deviation coincides with a great depression extending to the height of land in which highly developed soil deposits are present. The deciduous hardwoods occur as outliers and are always found on the better soils. Although the writer has not been able to study the Saugenay basin personally, it may be ventured that the northward migration of *Acer* at this point is also to be explained on the basis of soil development. BRAY (5) has found difficulty in explaining the occurrence of such trees as *Abies* and *Picea* in the swamps of New York. The soil in such localities is in a primitive stage of development. Although much humus has accumulated, there has been little or no intermingling of rock soil and humus, and the degree of aeration is low. The soil has been protected from the action of atmospheric agencies and running water, hence its undeveloped condition. The result is the same as when the slowly weathering Laurentian rock resists the agencies which promote soil formation. The fact that the same forest species are present in both places emphasizes the potency of the rate of soil development as a factor in the determination of tree distribution.

The evidence submitted is regarded as sufficient to prove that throughout a great region of Ontario dominated by *Picea* and *Abies* these genera are not permanent or climax forms, since they are replaced by *Acer* when soil conditions become favorable. WHITFORD (25), after studying the forests of Michigan, states that soils are improved by coniferous trees, and when sufficient humus soil has accumulated the deciduous species establish themselves. BRAY (5) also implies this relation. COOPER (6), however, after a study of Isle Royal, comes to the conclusion that "this type (*Abies-Picea-Betula* forest) is the climax forest of that portion of the northeastern conifer region under consideration; in other words, upon Isle Royal it is the final and permanent vegetative stage toward the establishment of which all other plant societies are successive steps. It is the climatic forest of the region, permanent while the climate remains essentially as now." The same paper records stands of *Acer* on certain ridges of Isle Royal and in other places where soil conditions seem particularly favorable. It seems probable that the occurrence of these stands might be explained on the basis of soil development.

It is evident from a study of the forests of northern Ontario that the deciduous hardwood forest is encroaching upon the coniferous forest region, and that the progress of this encroachment has lagged behind temperature changes, being now dependent principally upon the rate of soil development.

The relation of shade to the time factor of distribution is in accord with the specific tolerance of a given species with respect to light. The *Acer-Picea* forest provides shade which is essential for *Acer* seedlings, while detrimental to *Picea* or *Abies* seedlings. The encroachment of the deciduous hardwood forest upon the coniferous forest, made possible by changes in temperature and soil development, is also promoted, and the result made more permanent by decreasing light intensity due to shade conditions.

The importance of methods of seed dispersal as an element of the time factor of distribution is obvious. Where changes in conditions are slow, for instance yearly temperature modifications, even the trees whose methods of dispersal allow them to migrate slowly

are able to keep pace, and where ecological changes are more rapid species having the best methods of seed dispersal naturally migrate most rapidly. The rapid invasion of a burned area by the *Populus-Betula* association is due primarily to the widespread dispersal of the seeds of these species. In contrast, *Pinus* takes its place among the trees which appear later, largely because it has a less efficient method of scattering seeds. A number of examples of the limitations of seed dispersal have been noted. In several cases where a burn had left only one or two pines upon an island the usual *Populus-Betula* association was unable to gain a foothold because of the distance from the mainland; hence these species were superseded by numerous pine seedlings. Doubtless the same principles may be applied to the relation between seed dispersal and tree migration even over greater areas. The time factor of distribution may be an expression of the rate of migration as it is determined by the method of seed dispersal.

The time factor of distribution is an expression of the rate of migration. The rate of migration is dependent upon such primary conditions as temperature, water supply, soil properties, light intensity, and methods of distribution. Time, as a condition of change in environmental factors, becomes itself of great importance in any consideration of the factors of forest distribution.

Competition factor

Competition results in the survival of the fittest. The fittest is that species or individual whose specific range of tolerance is best related to the environmental condition acting as a limiting factor toward other species; hence temperature, water supply, soil, or light may act as the basis of competition. Time may also act as a basis of competition, since it changes conditions in environmental factors. In order that competition may act as a distributional factor, conditions must be favorable for one or more species and unfavorable for others. While the time factor is an expression of the rate of change of the environmental factor acting in a limiting capacity, the competition factor is an expression of the relation between the ranges of tolerance of the forms in question toward the limiting environmental factor.

The encroachment of the deciduous hardwood forest of Ontario upon the coniferous forest is accompanied by competition. The progressive changes in such conditions as humus content of the soil and light intensity are such as to increasingly favor the former association to the detriment of the latter. *Abies*, for instance, grows readily on good soil, but it cannot tolerate the shade of an *Acer* forest. The competition becomes too great; in other words, the changes in environmental factors have been such that the mean of the range of tolerance of *Acer* more closely approximates existing conditions than that of *Abies*. The factor of competition plays its chief rôle in the so-called transition areas, where the specific ranges of tolerance of the species concerned all include existing conditions although unequally. That species dominates, other things being equal, whose mean of tolerance more nearly approximates environmental conditions.

Specific ranges of tolerance

The specific ranges of tolerance of some of the dominant forest species of Ontario, together with their relation to limiting factors, will be considered. Many of the data are represented diagrammatically in the accompanying diagrams (figs. 3-6). These diagrams summarize data collected regarding the specific ranges of tolerance of a number of forest species. In preparing the temperature diagrams (fig. 3), for example, other factors have been eliminated by selecting data respecting localities where other conditions have been favorable; in this way the maxima and minima have been determined. The diagrams are relative rather than quantitative, hence they suggest a field of research which would supply absolute numbers. When the maxima and minima have been determined, the means are represented by the mid-points of the lines joining these extremes. The radii of the circles of which the lines joining the extremes are diameters represent the magnitudes of the specific ranges of tolerance. The comparative areas of distribution as determined by the several limiting factors are represented, theoretically, by circles whose centers are the means of their ranges of tolerance and whose radii are the lines representing those ranges.

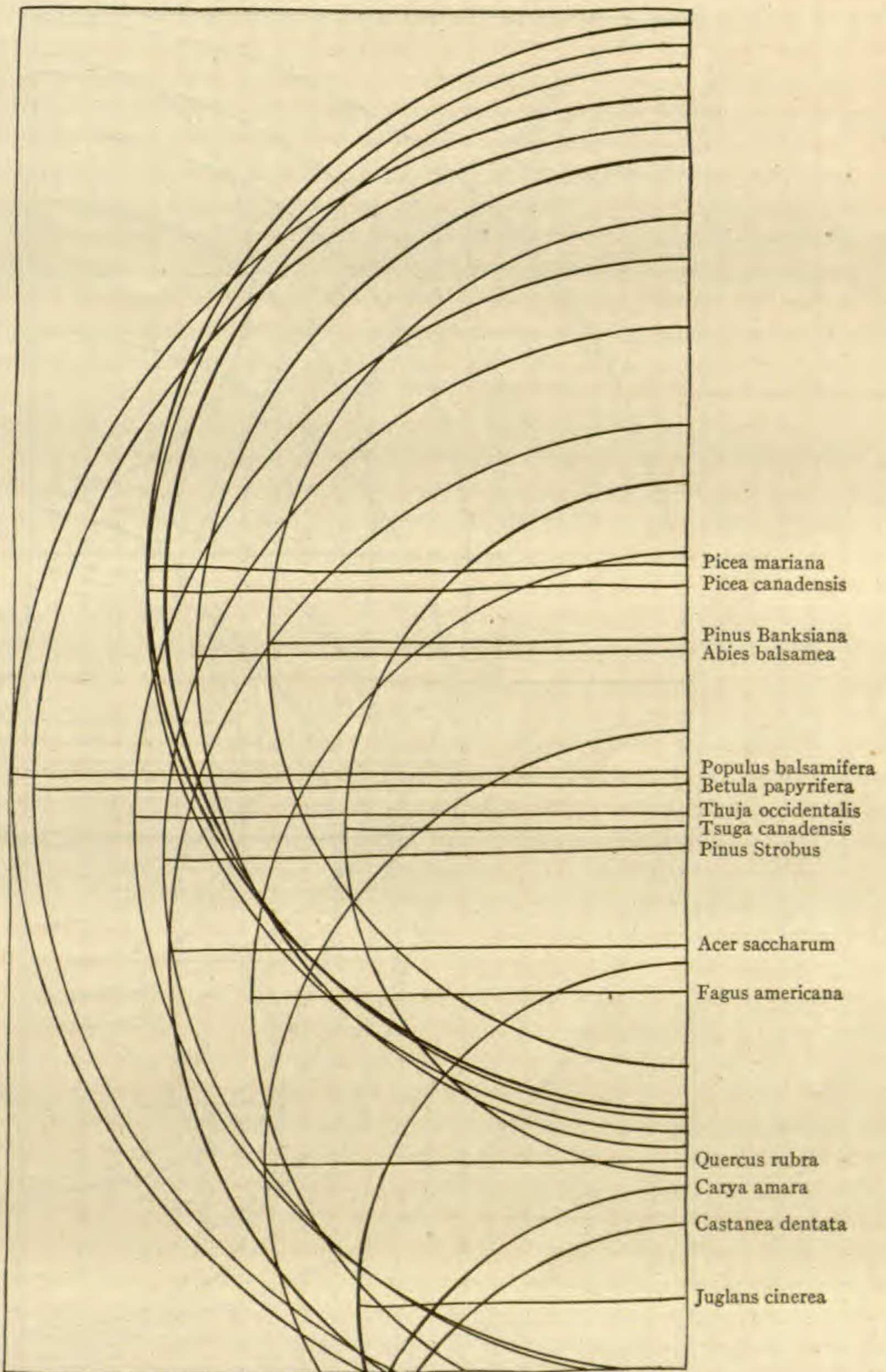


FIG. 3.—Forest trees: specific ranges of tolerance with respect to temperature

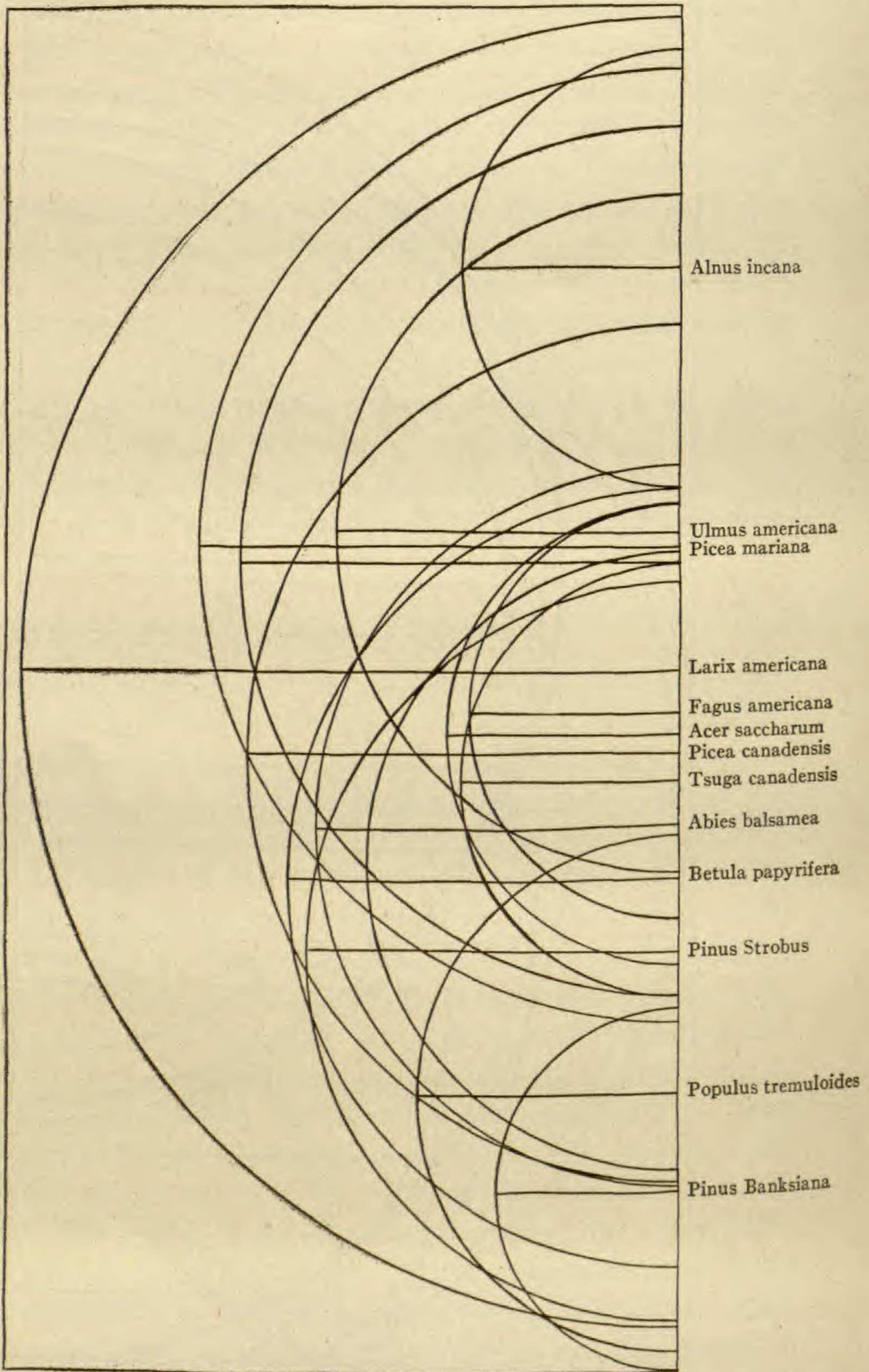


FIG. 4.—Forest trees: specific ranges of tolerance with respect to water

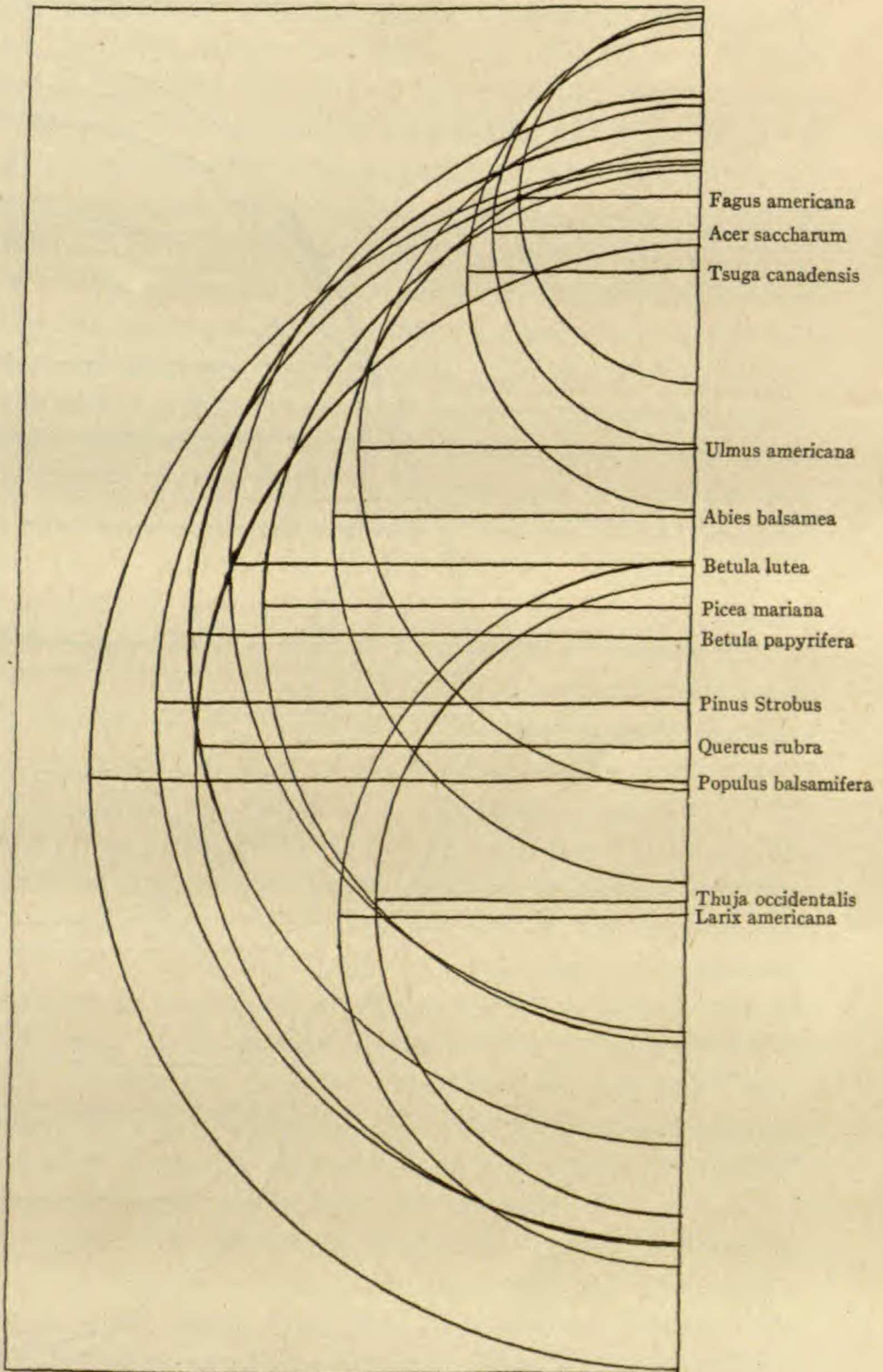


FIG. 5.—Forest trees: specific ranges of tolerance with respect to soil development

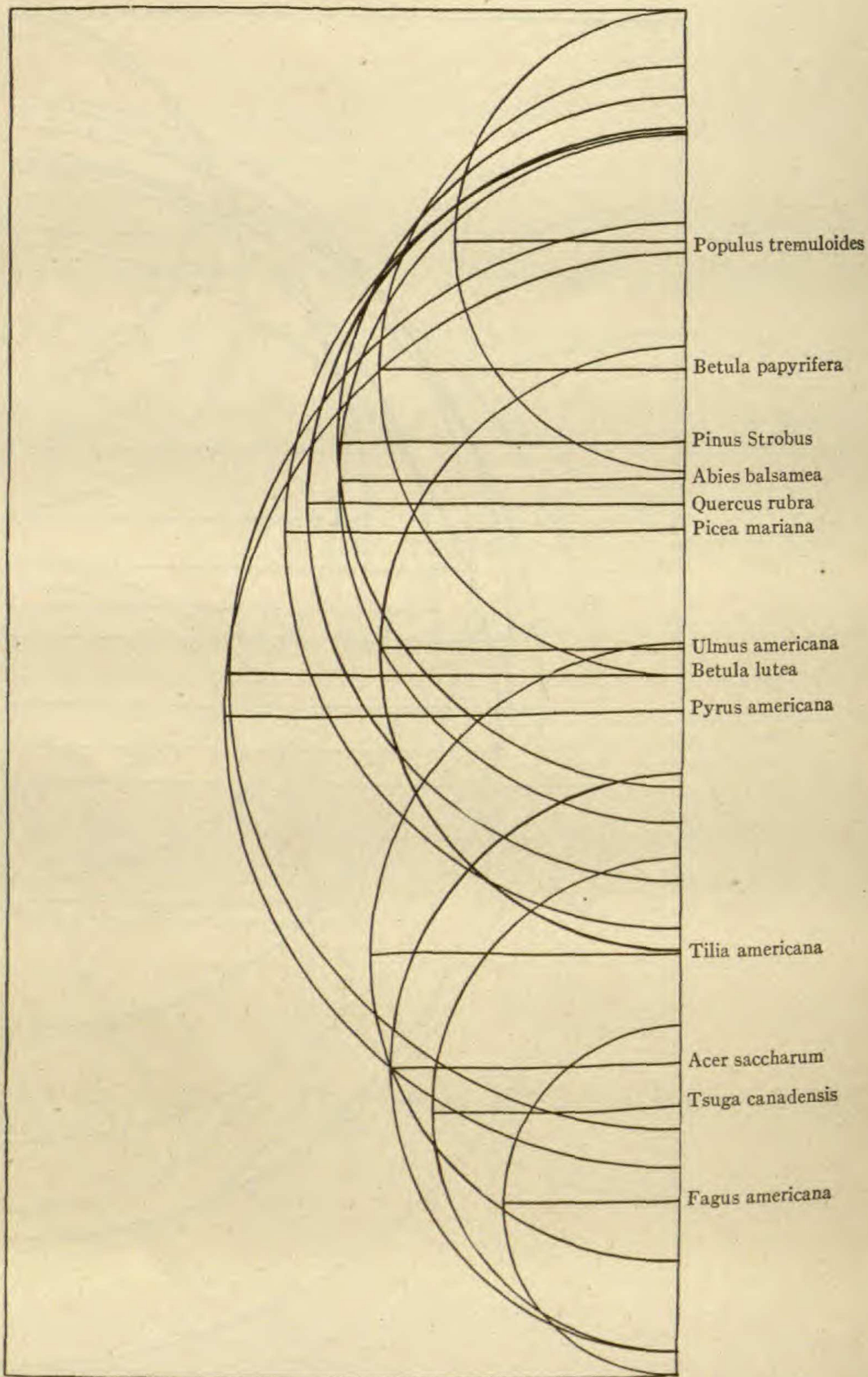


FIG. 6.—Forest trees: specific ranges of tolerance with respect to intensity of light

ABIES BALSAMEA.—*Physical factors*.—"Moisture and temperature are the main factors influencing the distribution of *Abies balsamea*; it requires a cold climate and a constant supply of moisture at its roots; a mean annual temperature not exceeding 40° F. with an average summer temperature of not more than 70° F. and a mean precipitation not less than 25 inches evenly distributed throughout the year are the necessary conditions for its growth" ZON (27). The maximum of its range of temperature tolerance is high, very closely approximating that of *Picea*; the minimum is lower than has generally been conceded, other factors having practically eliminated it from the warmer regions of its normal temperature range. While *Abies balsamea* normally has a wide water range, it seldom thrives except in a moist soil because this hinders the growth of a fungus which in a drier soil attacks the roots ("ground rot"). Southward *Abies balsamea* "attains its best growth and largest sizes on flats the soil of which is usually a moist deep sand loam" (ZON 27), while "southwest of Hudson Bay it grows only in the warmest and best soils and is entirely wanting in the cold swampy tracts" (LOW 18). *A. balsamea* demands comparatively high light intensity; seedlings are seldom found except in clearings caused by windfall, or otherwise. Generally, *Abies* has a wide range of tolerance.

Competition factor.—Northward *Picea* is the chief competitor of *Abies*; their ranges of tolerance are similar, the maxima and minima of *Picea* generally being more extreme; consequently *Abies* under most conditions would be secondary were it not for the fact that near the mean of their ranges *Abies* grows more rapidly than *Picea*. Southward the chief competitors are *Acer* and *Tsuga*. These forms have the advantage of being more shade tolerant, and hence they gradually encroach upon and finally exterminate *Abies*, which demands greater light intensity (fig. 7).

Time factor.—The northward migration of *Abies balsamea* is conditioned by temperature, and since the magnitude of temperature changes is dependent upon time, it is evident that the time factor has a bearing upon distribution. The distribution southward is affected by competition of such forms as *Acer* and *Tsuga*. Time is necessary for the environmental changes which produce

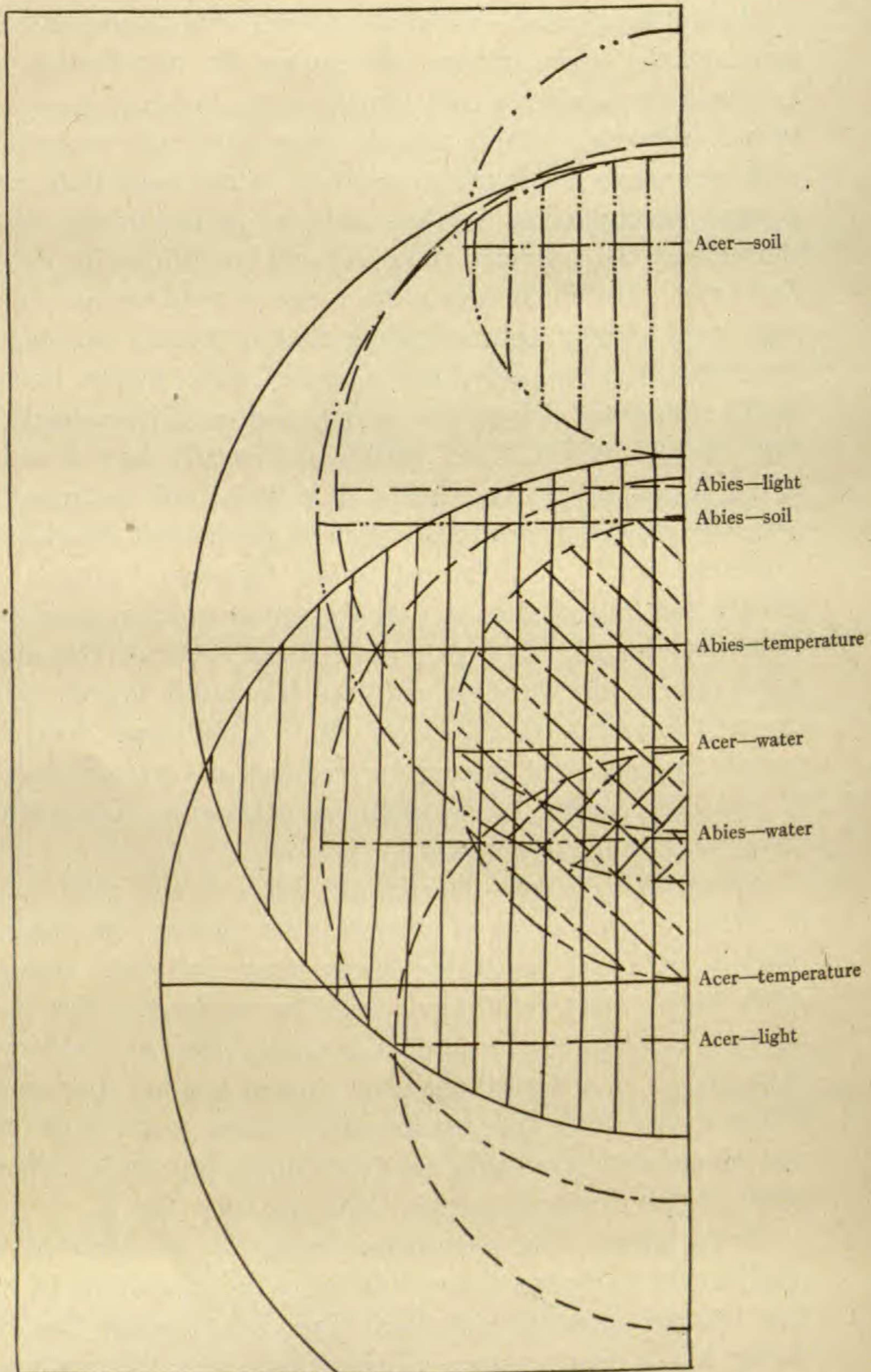


FIG. 7.—Competition areas of *Abies balsamea* and *Acer saccharum* shown by superimposing specific areas of tolerance toward factors of temperature, water, soil, and light; overlapping areas barred, the bars being similar to radii representing ranges of tolerance; barred areas represent areas of competition.

conditions more nearly approximating the mean of the range of tolerance of these competitors, thereby contributing toward the elimination of *Abies*.

The problem which arises by the appearance of *Abies* in swamps south of its "normal" range may be explained by regarding soil rather than temperature as the limiting factor. Soil changes have been slower in the undisturbed humus and rock soil layers of the swamp than on the weathered uplands. Soil conditions approximating the mean of the range for *Abies* have been maintained, hence this form has persisted; also, the presence of abundant water inhibits the attacks of parasitic fungi, thereby permitting the growth of *Abies*.

PICEA MARIANA AND P. CANADENSIS.—Although these species are closely related morphologically, they are quite different ecologically; in this respect *P. canadensis* is quite closely associated with *Abies balsamea*. *P. mariana* has a wider range of tolerance than either. Low states, "In Labrador (and northern Quebec) the white spruce grows on rich intervale grounds or near the shores of lakes and rivers. The black spruce is found on hills and in cold swamps. The two kinds have the same geographical range northward." Soil development and soil water frequently become limiting factors, separating these species. The status of temperature as a factor in distribution is demonstrated by the differences existing between *Picea mariana* and *P. canadensis*. Although they have practically the same temperature range, the latter is not found throughout a vast area of the region lying between Hudson Bay and Labrador. Available accounts and the evidence given by its habitat in other regions indicate that soil development is the limiting factor. In this respect *Abies balsamea* takes a position intermediate between these two species of *Picea*. *Picea* has previously been referred to as the chief competitor of *Abies*.

LARIX AMERICANA.—This species has a very wide range of tolerance toward temperature, water, and soil conditions. BELL (2) states "That it has an equally thrifty growth in the country to the south of James Bay and westward toward Lake Winnipeg. In this great region it attains its greatest perfection in the dry uplands and in good soil near the rivers, but smaller trees with small

black spruces grow everywhere on the low swampy grounds. South of the Ottawa River it grows principally on low and level land." Low states, "*Larix* is probably the hardiest tree of the subarctic forest belt. Throughout the interior it is found in all the cold swamps and is always the largest tree in the vicinity. Along the northern margin of the forest the larch continues a tree to the very edge where the black spruce is dwarfed to a mere shrub. *Larix* demonstrates the principle that a tree which has a wide range of tolerance does not flourish in competition with species of smaller range, but is crowded into situations where conditions exclude competitors. Such a form is usually of slow growth compared with forms which are more specialized. *Larix* cannot be called a xerophyte, a hydrophyte, or a mesophyte, since it may be any of the three. Although it is usually found under extreme conditions, it grows best under mean conditions, provided competitors have been eliminated. The distribution of *Larix* is accounted for by its wide range of tolerance, together with its low status in the competition scale."

THUJA OCCIDENTALIS.—The "anomalous" distribution of *Thuja occidentalis* defies explanation by regarding temperature, water, or soil as the limiting factors (figs. 1, 2). "It is absent in Newfoundland, Cape Breton, Nova Scotia, and the east half of Prince Edward Island, but unusually large and fine in New Brunswick and the Gaspé peninsula, in which the climate, soil, etc., are the same as in the adjacent regions, where no trace of the species is to be found." BELL (2) also states that "there is a remarkable outlier of white cedar brushwood around Cedar Lake on the upper part of the Saskatchewan River at a distance of 190 miles to the northwest of the nearest point of the main area covered by this species." Moreover, it is notable that throughout great areas, for instance the Temagami region, *Thuja* is unknown, while in the surrounding country it is abundant. *T. occidentalis* has a wide range of tolerance toward environmental conditions. The presence of "outliers" where conditions are similar to those prevailing in other regions where it ordinarily occurs indicates that the general area of its distribution does not extend to its ecological limit, in many instances at least. The northern area of its distribution is

roughly outlined by a semicircle, a fact which contributes evidence that *Thuja* has migrated radiately from a limited area. The method of reproduction is such that it does not migrate rapidly; that a great proportion of seeds fail to develop is of importance in this connection. It would seem that the migration of this form has lagged behind changes in ecological conditions. With respect to its range of tolerance and its position in the scale of competitors under mean conditions, *Thuja* resembles *Larix*. These characters, together with the limiting action of time, account for most of the facts of its distribution.

PINUS BANKSIANA.—The tolerance of this form toward low temperatures, dry conditions, and soil poor in humus, together with its limited range toward the other extremes, place it in a unique place among the trees of the northwestern region. It is practically eliminated from the low lying lands to the south and west of Hudson Bay and James Bay, water being the limiting factor. The inconsistencies in accounts of its northward distribution in this region are the result of its occasional presence where there are higher lands between rivers. It extends northward to 56° N. lat. on the dry uplands east of Hudson Bay. Farther south, also, it is to be found only on dry rocky or sandy soil containing little humus. It is one of the pioneer forms and survives where it can avoid competition by enduring severe conditions.

PINUS STROBUS.—This species is also a pioneer among the conifers. Seedlings are seldom found except where there is a high light intensity and well drained soil. Its ranges of tolerance with respect to temperature and water do not include the extremes which characterize *P. Banksiana*. The northern limit follows a yearly isotherm (33° F.) very closely. It would seem that in this case temperature acts as a limiting factor. Because of its longevity and its towering height individuals or groves of mature trees often persist in a region where seedlings have long been eliminated by other forms which are higher in the competition scale. The pine forest is normally succeeded by such forms as *Tsuga* or *Acer* whose seedlings tolerated shade, the time factor; hence its perpetuation depends upon the maintenance of or reversion to pioneer conditions.

TSUGA CANADENSIS.—This species is among conifers what *Acer* and *Fagus* are among deciduous trees; it is a climax form. In fact, its ranges of tolerance are almost identical with those of the deciduous forms already mentioned. *T. canadensis*, when contrasted with such species as are represented by *Pinus Banksiana*, serves to emphasize the ecological diversity of conifers. BELL (2) states that “this tree maintains a good size to the verge of its range and always appears to terminate abruptly.” Stands of mature trees are to be found as “outliers” beyond the general area of its distribution. This evidence confirms the belief that *Tsuga* is still migrating; that in many instances it has been limited by the time factor rather than by environmental factors.

POPULUS BALSAMIFERA AND *P. TREMULOIDES*.—Although *P. balsamifera* generally extends farther north than *P. tremuloides*, having a greater temperature range of tolerance, its northern limit passes south of the latter at 71° W. long.; soil becomes the limiting factor in this region. *P. balsamifera* “appears to confine itself to heavy clay soil of the river valleys on the modified drift of the Cambrian areas” (Low 18), while “*P. tremuloides* is most plentiful on the unmodified glacial till of the drift ridges.” The seedlings of both require a high degree of light intensity, and as such are pioneer forms. Southward they occur only where fire and other destructive agencies have restored pioneer conditions. The abundance of these species of *Populus* northward, especially south and west from Hudson Bay, would indicate that this region is biologically young.

ACER SACCHARUM.—South of the Laurentian Plateau *A. saccharum* dominates, except in the undrained lowlands. Its range of tolerance is limited to a mature soil (that is, well drained, well aerated, and containing a relatively large amount of humus intimately mixed with the rock soil) and low light intensity. The humidity of the atmosphere in Ontario is such that it is doubtful whether it ever acts as a limiting factor, other conditions being favorable. It is evident that the distribution of *Acer* is chiefly an expression of the time factor; the time required to give rise to a deep, well drained humus soil and to shade conditions, and in addition the time which is necessary to crowd out those forms which

have been instrumental in providing such conditions. As mentioned before (under time factor), the time rate of change has been less in the lowlands and upon the rock outcrops of the Laurentian Plateau than upon the highland and the weathered glacial moraine. There is abundant evidence that *Acer* is migrating northward, its progress being contingent upon the time rate of soil development.

FAGUS AMERICANA.—This species has a range of tolerance toward soil conditions which is even more limited than that of *Acer*. What has already been said for *Acer* applies equally for *Fagus*, since the latter is closely associated with the former.

ULMUS AMERICANA.—This species is another form whose distribution defies explanation by considering either temperature or rainfall as limiting factors. The limit extends well into the plains and northward beyond Lake Winnipeg; it swings southward, then northward again in the region south of James Bay; then abruptly southward and again northward with no apparent dependence upon temperature or precipitation conditions. Even within its general limits it is found only where there is a clay, imperfectly drained soil; over large areas, especially throughout the Laurentian Plateau, it has not been found. "On the Missinabi or west branch of the Moose River the white elm reappears 130 miles north of its general boundary on descending to a sufficiently low elevation above the sea" (BELL 2). Soil conditions are the chief limiting factors; on the clay soil of the lowlands, where there is poor drainage, is its favorite habitat; for this reason it is intermittingly distributed. Its reappearance north of the height of land, its occurrence in the lowlands about Lake Winnipeg, as well as many other eccentricities of this species, may be explained upon this basis.

BETULA LUTEA.—This species may be associated with pioneer forms such as *B. papyrifera* or climax forms such as *Acer*. "Yellow birch is the most abundant hardwood in New England" (12), while in the lake region it is seldom seen; it becomes more abundant in the Laurentian region. "It grows in forests of widely different composition and shares to some extent the habits of paper birch, appearing on burns in small even-aged stands" (12). The seedlings are pioneer, yet, because of its comparative longevity,